THE MOSCHOPID SKULLS IN THE SOUTH AFRICAN MUSEUM

BY

Lieuwe Dirk Boonstra
South African Museum

(With eleven text-figures)

Contents

Introduction

All the known specimens of the South African Moschopids, with the single exception of *Moschoides*—housed in the Walker Museum of the University of Chicago, have been personally examined. In addition to these there are in the collection of the South African Museum a number of cranial specimens found as isolated specimens at various locations in the Koup, and lastly the skulls of at least twenty individuals found together at Kruisvlei in a thin layer of argillaceous sandstone.

Historical

Delphinognathus conocephalus, described in 1892 by Seeley, was the first South African Moschopid to become known. Although some of the structures were misinterpreted, Seeley's woodcuts excellently portray the parts of the skull preserved. Of this skull Broom in 1910 published a restored figure which is inaccurate in a number of respects.

Nineteen years later the second genus, *Moschops*, was described by Broom (1911), the type being an incomplete skull. This Spitskop material, found by Whaits and sold by Broom to the American Museum, includes a number of topotype skulls. These skulls were subsequently studied by Gregory in 1926 and by the author in 1936.

The third genus, *Moschognathus*, was founded by Broom in 1914 on a lower jaw found by Whaits near Beaufort West and this jaw, together with the postcranial skeleton, was restudied by Gregory in 1926.

In 1914 Watson founded two additional genera, *Pnigalion* and *Lamiasaurus*, on rather poor material. As *Lamiasaurus* has as type specimen a snout which

is Titanosuchian and a postorbital skull piece which is Moschopid, it has been proposed that only the snout be considered as the type and this has been found to be at most a doubtful species of the genus *Titanosuchus*. The postorbital skull piece is best left unnamed.

In 1937 Byrne founded the genus *Moschoides* on a fair skeleton with which is associated four fragments with teeth. Finally in 1952 I described a fairly good skull from Kruisvlei under the name *Avenantia kruisvleiensis*.

General Shape and Form of the Skull

The Moschopid skull is fairly light to massive and of moderate size (length 308–423 mm., width 200–395 mm., height 216–309 mm.). The snout is relatively weak, very short and fairly high (preorbital length 160–195 mm., height 108–162 mm., width 114–222 mm.).

The orbit, which is fairly small to fairly large, does not lie wholly in the posterior half of the skull (with the possible exception of *Delphinognathus*). The bones of the preorbital part of the skull are only moderately thick, whereas those of the posterior half, particularly of the cranial roof, are fairly to greatly pachyostosed: in the latter the surface is fairly smooth to rough, whereas in the former it is smooth to fairly rough. In most, except *Delphinognathus*, the 'cheek' is also thickened and fairly rough. The pachyostosis of the cranial roof is in *Delphinognathus* greatest round the pineal foramen, but in the other genera it is general and no distinct naso-frontal boss is developed. There is also no step between the facial and cranial surfaces, as these surfaces run into each other in an even convexity. The postfrontal bone is fairly light to massive and never has a boss. The orbits, except in *Delphinognathus*, are fairly small and look forwards and outwards, dorsally overhung and posteriorly bounded by the greatly thickened orbital rim.

The temporal fossa is wide and roomy in *Avenantia*, with a moderate antero-posterior diameter in *Delphinognathus* and narrow and slit-like in *Moschops*.

The interparietal width is small to large (54–198 mm.), with a parietal crista present in *Avenantia*.

Due to the forward position of the quadrate and the short snout, the lower jaw is short and the gape small.

Bones of the Dorsal and Lateral Surfaces

The premaxillaries (P.M.) form the anterior part of the upper median surface; they stretch backwards from the anterior alveolar border to end well anterior to the plane in which the anterior orbital border lies; posteriorly they lie in a groove in the nasals which bones further posteriorly, meeting each other in the median line, prevent the premaxillaries from meeting the frontals (my 1936 account on this feature in A.M.N.H. 5553 is thus incorrect and Efremov's criticism justified). Broad anteriorly up to the anterior edge of the *naris*, the premaxillaries narrow abruptly and then taper in posterior direction,

but the internarial bar is strong. The surface of the premaxillaries in the median line curves evenly dorso-posteriorly and this slope is continued, without any step, on to the nasals and frontals.

The nasals (N.) together present a U-shaped surface with the limbs of the U directed anteriorly and the premaxillaries wedged in between the limbs and posteriorly lying in a groove in the nasals, anteriorly each nasal forms the posterior border of the *naris* and meets the posterior edge of the septomaxilla; posterior to the limits of the premaxillaries the two nasals meet in the median line and meet the anterior ends of the frontals, but although the bones are here greatly thickened there is no indication of any distinct naso-frontal boss, and the sweep of the upper surface is a gentle convexity with no indication of a step between the facial and cranial surfaces; there is no depression in the posterior nasal surface for a facial gland as there is in most of the Tapinocephalidae. Laterally the swollen surface of the nasal curves evenly into that of the strongly swollen prefrontal. A tongue of the frontal sometimes separates the posterior part of the prefrontal from the nasal.

The septomaxilla (S.M.) has a small facial exposure; it forms the lateral and part of the anterior and posterior borders of the *naris*; its surface within the *naris*, of which it forms the floor, is extensive. I have not located a septomaxillary foramen.

The maxilla (M.) is the largest bone of the face; although fairly short it is quite high; its posterior edge is weakly indented to receive the very short lacrimal, so that both the dorsal and the ventral processes appear to be short; the dorsal process is short and wide and posteriorly truncated to meet the prefrontal in a long suture; the ventral process is longer and tapers to a point along its short suture with the jugal; the anterior half of the alveolar edge curves gently upwards to where it meets the premaxilla.

The lacrimal (L.) has a small facial exposure; it is very short, but high and in outline presents a face which is a crescent with the tips cut off; it thus forms most of the anterior orbital rim, which though rounded is not much thickened. It is only slightly overhung by the prefrontals and has no contact with the nasal because of the intercalation of the strong dorsal process of the maxilla. No foramen is visible on the facial surface as this probably lies within the orbit.

The jugal (J.) is quite a strong bone but like the bones of the snout is but little pachystosed and its surface is fairly smooth; it forms the ventral, relatively unthickened, border of the orbit. From its contact with the maxilla, its ventral edge sweeps down sharply postero-ventrally to where it makes a small contact with the upper edge of the quadratojugal (but in *Delphinognathus* the posterior part of its ventral edge is deeply excavated to form a deep and roomy indentation breaking the even sweep of the antero-ventral border of the jugal on to the anterior face of the quadratojugal, whereas in *Moschops* and *Avenantia* this sweep is only interrupted by a slight nick at the junction of these two bones (this is also evident in some Struthiocephalids). The posterior edge of the jugal is slightly (*Avenantia*) or deeply indented by the anterior process of the squamosal

so that the face of the postero-ventral process of the jugal is long and narrow, except in *Avenantia* when it is short and broad. Its contact with the postorbital is along a short curved suture.

The prefrontal (Pr.F.) is only moderately to strongly thickened; it forms the moderate to thick antero-dorsal part of the orbital border which overhangs the orbit moderately to strongly. In its anterior part, where it meets the lacrimal and maxilla, it is less swollen and its surface is smoother than in its posterior parts, and it does not strongly overhang the lacrimal. In all the Moschopid genera the prefrontal meets the maxilla and the lacrimal is thus excluded from contact with the nasal. In dorsal view its width is seen to vary, this also in specimens of the same genus. Posteriorly it usually does not meet the postfrontal, but in *Avenantia* it just meets the postfrontal, so the frontal just enters the orbital border or is just excluded from it. Medially a varying tongue of the frontal is sometimes wedged in between the nasal and prefrontal, but this tongue is sometimes absent. The swollen surface of the prefrontal passes evenly on to the swollen surfaces of the nasal and frontal and no groove is ever developed to prevent this confluence as in some Tapinocephalids and Struthiocephalids.

The frontal (F.) is the largest bone of the dorsal skull roof, being particularly large in *Moschops koupensis*. The pair together forms a roughly rectangular surface as the main body of the two bones, with, laterally, a tongue which just enters or is just excluded from the orbital border and anteriorly, there is in some specimens a varying tongue wedged in between the posterior end of the nasal and the prefrontal. The frontals meet the parietals in a nearly straight transverse suture, but in *Moschops koupensis* the parietals form a strong anteriorly directed wedge into the frontals. Sometimes a postero-laterally directed tongue separates the postfrontal from the parietal, but usually there is a fair to small contact between parietal and postfrontal. Anteriorly the thickened frontal surface flows with a gentle curve on to that of the nasal so that there is no indication whatever of a distinct naso-frontal boss. The frontal surface is similarly confluent with that of the parietals and postfrontals. Although in general the frontal face is domed there is in some forms a depression along the middle line, slight in some specimens of *M. capensis*, but in *Avenantia* it forms a decided wide but fairly shallow longitudinal groove. The pachyostosis along the line of junction of the two frontals is thus, in some specimens, less developed than more laterally.

The postfrontal (Po.F.) is a fair-sized bone moderately to very strongly thickened; it forms a small to fairly large part of the dorso-posterior section of the orbital border; it sometimes meets the prefrontal but more often the lateral tongue of the frontal is intercalated between these two bones; posteriorly it meets the parietal in most specimens, but sometimes the postero-lateral tongue of the frontal intervenes; stretching from the orbit to the temporal fossa it forms the upper part of the postorbital bar lying above the postorbital and latero-ventral to the frontal. The postfrontal, though moderately to very strongly pachyostosed, never forms a distinct boss, but has its rough outer surface

confluent with the swelling of the frontal, parietal and postorbital in an even gentle convexity.

The parietal (P.) of the Moschopids is a remarkably variable element, not so much in regard to its connections with and relationships to the contiguous bones as in the shape and topography of its upper face.

In *Moschops koupensis* and in some specimens of *M. capensis* it forms and completes the general dome-shaped convexity of the upper cranial roof coalescing in gentle curves with the greatly pachyostosed surrounding bones. Whereas in other specimens of *Moschops capensis* there is a tendency, more or less pronounced, for it to form a mound around the pineal foramen, and, in one greatly distorted and probably young skull, this mound approaches the conical shape seen in *Delphinognathus*.

In *Avenantia* the parietal is but little pachyostosed; there is a circular and prominent wall around the pineal foramen, with a lateral excavation bounded by a ridge lying still further laterally; posteriorly the bone forms a low, fairly narrow crista which curves down towards the occiput, whereas in *Moschops* the parietal posterior to the foramen tends to form a groove along the median line more or less strongly developed.

In *Moschops koupensis* the parietal forms the posterior edge of the skull between the interparietal and the tabular, whereas in all the other forms the posterior edge is wholly formed by the interparietal and the two tabulars; this is due to the parietal curving down postero-ventrally much more strongly.

As a pair the parietals form a much smaller part of the cranial roof than do the two frontals. A moderate to large pineal foramen lies very near to fairly far away from the frontal suture but it is always well anterior of the occipital edge. The size of the pineal foramen varies within the same species and a greater size does not appear to be correlated with juvenility.

There is considerable variation in antero-posterior length of the parietal; the fronto-parietal suture is either a fairly straight transverse line or forms an anteriorly directed obtuse or sharp V; the parietal meets or does not meet the postfrontal. Posteriorly the parietals meet the interparietal and tabulars in a fairly straight or slightly curved suture, but in *M. koupensis* this general curve is indented where it makes contact with the interparietal.

The parietal width in the Moschopids shows considerable variation, which, within the species *Moschops capensis*, appears to be due to differences of age in some cases, but where other features exclude this explanation it can only be due to differences in sex. In *M. capensis* the parietal width varies from 108 to 172 mm.; in *M. koupensis* it is 198 mm.; in *Delphinognathus* 120 mm., and in *Avenantia* 84 mm. (with the crista 48 mm. at its narrowest part). In some skulls of *M. capensis* there is some indication of a pinching-in across the parietals to form a dorsal bay to the temporal fossa as in some species of *Struthiocephalus* and *Keratocephalus*.

The parietal forms a rounded ill-defined edge to the upper border of the temporal fossa in all the forms, except in *Avenantia* where the edge of the crista

forms this edge; lateral to this the parietal forms a more or less vertical face within the temporal fossa with its ventral edge meeting the posterior end of the postorbital and the dorsal edge of the upsweeping squamosal.

Except in *Avenantia* the parietal of the Moschopids does not send a tapering process on to the posttemporal arch intercalated between the tabular and the squamosal, as is the case in Tapinocephalids and Struthiocephalids. This confirms my observation (1936) on the Spitskop material in the American Museum and Efremov's (1940) stricture on this observation is thus groundless. The mistake made by Efremov is that he made no allowance for the possibility that the postero-lateral tongue of the parietal may, by increased pachyostosis of the contiguous bones, be overgrown by them. This in fact is just what has taken place in *Moschops*.

The postorbital (P.O.) is a moderate to very massive bone forming the lower part of the postorbital bar and with a much more lightly built posterior flange lining part of the upper wall of the temporal fossa; anteriorly it forms a small to great part of the thickened posterior orbital border, and posteriorly most of the thick to very thick anterior border of the temporal fossa. Ventrally it abuts against the squamosal in a long curved suture and, except in *Avenantia*, meets the jugal along a short curved suture. Dorsally it meets the lower edge of the postfrontal along a curved suture running across the postorbital bar. Within the temporal fossa the postorbital sends a short to moderately long lightly built flange upwards and backwards to flank the lateral face of the parietal and to meet the dorsal edge of the upsweeping squamosal within the temporal fossa. These two bones together with the lateral face of the parietal thus form the median lining of the temporal fossa.

The squamosal (Sq.) is large and is the main constituent bone of the 'cheek'; it is little to greatly thickened with its outer face fairly flat and smooth in *Delphinognathus*, but more or less swollen and rough in the other genera. Anteriorly it meets the jugal in a squamous suture, fairly straight in *Avenantia*, moderately indented in *Pnigalion* and deeply indented in *Moschops* and *Delphinognathus* so that it lies over the upper edge of the postero-ventrally directed process of the jugal. In its antero-ventral corner it receives the quadratojugal overlapping the posterior part of this bone's outer face. Dorsally its anterior part forms the base of the postorbital bar and here it is overlapped by the postorbital and further posteriorly the squamosal forms the fairly thin to thick lower border of the temporal fossa and then, sweeping upwards, forms most of the posttemporal arch and the posterior border of the temporal fossa. From the posterior edge of the temporal fossa the squamosal curves inwards and forwards to meet the parietal and postorbital inside the upper part of the temporal fossa.

On the outer face of the posttemporal arch the squamosal meets the tabular and in the Moschopids there is no long tongue-like process of the parietal intercalated between the squamosal and the tabular, but in *Avenantia* there is a short wedge of the parietal between these two bones.

Postero-ventrally the thick rounded edge of the squamosal forms the edge of the skull and then on the posterior face carries the 'auditory groove', which is bounded medially by a scroll-like ridge.

The tabular (T.) in dorsal view presents only its upper edge, which is thin in *Avenantia* but thick in *Moschops* where it has overgrown the postero-lateral tongue of the parietal. In lateral view the tabular is seen to form most of the posterior edge of the skull above the squamosal.

The interparietal (I.P.) in dorsal view presents only its dorsal edge which forms the median part of the occipital edge. The dorsal interparietal edge is thin in *Avenantia*, fairly thick in *Moschops capensis* and in *M. koupensis* forms only a small part of the dorsal edge in the median line where the dorsal surface of the skull is grooved; laterally to it the parietal forms the posterior edge until it meets the tabular.

The quadratojugal (Q.J.) in lateral view, presents a narrow dorso-ventrally elongated face in *Moschops* where it is directed antero-ventrally. Dorsally it forms a weak contact with the jugal, with a slight narrow notch between these two bones anteriorly. In most specimens of *Moschops* the squamosal overlaps the posterior border of the quadratojugal, but in one specimen the squamosal also clasps the quadratojugal dorsally so that it is partly wedged in to the squamosal, but the quadratojugal never forms a narrow deep wedge into the squamosal as in Tapinocephalids.

In *Delphinognathus* the anterior half of the upper end of the quadratojugal is deeply notched and concomitantly the anterior half of the lower end of the jugal is also notched so that a deep broad notch is formed between these two bones. The posterior half of the upper end of the quadratojugal meets the posterior half of the lower end of the jugal as in *Moschops*. The lateral surface of the quadratojugal is thus not narrow and elongated as in *Moschops* but can be described as an elongated dorso-ventrally directed surface with wedge-shaped anterior process. According to Watson (1914) the quadratojugal in *Pnigalion* presents a large, roughly quadrangular outer surface meeting the jugal along a fairly long suture and not wedged into the squamosal.

The quadrate (Q.) can in lateral view be seen lying medially to the quadratojugal with the outer cotylus showing below the ventral limit of the quadratojugal, but in *M. koupensis* much of the antero-lateral surface of the quadrate above the cotylus is also visible in lateral view.

The Occiput

The occiput in the Moschopidae presents a fairly large surface, which is at least twice as broad as high and is shallowly concave from side to side. The dorsal edge of the occipital plate lies further posteriorly than the ventral edge. Along the median line there is a weak to fairly weak ridge on the interparietal. On either side of this ridge lies a shallow to moderately deep depression. The upper edge of the occipital plate proper lies high in most forms with a rounded edge, but in *Moschops koupensis* both the upper and lateral edges form a rampart-

like wall enclosing the inner part of the plate and encroaching on it so that the occipital plate proper becomes very small. The condyle is directed postero-ventrally so that the skull forms a sharp angle with the neck; it is a stout rounded knob dorsally excavated by a groove, sometimes quite deep, for the *medulla*; the lateral parts of the knob are formed by the exoccipitals.

The *foramen magnum* is large and oval or is fairly small with its sides pinched in. The posttemporal fossae are small with, in one case, a median groove leading into them; they are bounded by the supraoccipital and paroccipital. The lateral border of the skull is formed by the swollen squamosal which more medially is excavated to form the 'auditory groove' and this is bounded medially by a prominent scroll-like ridge wholly formed by the squamosal. Ventrally, the condyles of the quadrates lie in a plane far anterior of the plane of the occiput.

Viewing the occiput at right angles to the plane in which the alveolar borders lie, much of the surface of the parietal, postfrontals, postorbitals and frontal is seen and the ventral edge is formed by the squamosal, quadratojugal, quadrate, quadrate ramus of the pterygoid, exoccipital and basioccipital.

The basioccipital (B.O.) in occipital view shows only a small surface, viz. an elongated strip along the middle line of the condyle; its upper part is excavated and this groove leads into the *foramen magnum*; near its lower border there lies a notochordal pit.

The exoccipitals (E.O.) form the lateral surfaces of the condyle separated by the above-mentioned strip of the basioccipital (but in *Avenantia* the two exoccipitals meet to form the lower border of the *foramen magnum*); from the condylar surface the exoccipital extends forwards and upwards to enter the occipital plate forming an irregular triangular surface lateral to the *foramen magnum* overlapping the supraoccipital and paroccipital; the ventral border of this sheet of the exoccipital is notched to allow for the exit of the tenth nerve; the exoccipital forms most of the lateral rim of the *foramen magnum*.

The supraoccipital (S.O.) is a low but broad bone; in its lower median part it forms the upper and sometimes also much of the lateral rim of the *foramen magnum*. Laterally it extends to the outer corner of the posttemporal fossa, or well lateral of this fossa, and forms the dorsal border of this fossa and above this it meets the tabular in an undulating suture; dorsally it meets the interparietal in a fairly straight to curved suture. Along its ventral edge it makes contact with the paroccipital on both sides of the posttemporal fossa (but in *Moschops koupensis* only medially of this fossa). The median ridge is low or absent on the supraoccipital, but is fairly prominent on the interparietal.

The interparietal or dermosupraoccipital (I.P.) is a moderately to large-sized element forming the upper part of the middle of the occipital plate. It is a rectangular element with the corners developed as wedge-like processes; along the median line it carries a fairly strong ridge and lateral to this the bone is slightly or quite deeply excavated. Dorsally the bone forms a strong rounded edge curving over to meet the parietal, but in *Moschops koupensis* the upper part

of the bone forms a very strong overhanging rampart, which is laterally continued by a similar overhanging of the tabular.

The tabular (T.) has the largest surface of all the occipital bones. Its outer edge, which forms the lateral and part of the dorsal limits of the occipital plate proper, is weakly rounded or is developed into a very massive overhanging rampart, which greatly encroaches on to the more inner part of the occipital plate greatly reducing this area. (This condition in *Moschops koupensis* is a much more advanced development than that shown in *Tapinocephalus*, where it is only incipient.)

Dorsally the tabular meets the parietal on the dorsal surface of the skull and is just excluded from or just enters the edge of the posttemporal fossa. Its outer edge meets the upsweeping dorsal process of the squamosal but is excluded from the 'auditory ridge' which lies wholly on the squamosal. The latero-ventral corner of the tabular overlaps the paroccipital lateral to the posttemporal fossa. Internally it meets the interparietal and supraoccipital along a long undulating suture and is just or well excluded from the edge of the posttemporal fossa.

The paroccipital (P.O.) is, in occipital view, seen to be a strong bar medially abutting against the basioccipital and overlapped by the flange of the exoccipital and laterally extends to meet the squamosal and here it is overlapped by the downsweeping corner of the large tabular and itself overlaps on to the posterior face of the quadrate, which it supports very firmly. The medio-ventral corner of the paroccipital is seen to descend and form the posterior part of the rim of the *fenestra ovalis*. Its dorsal edge meets the supraoccipital except at the posttemporal fossa. In *Moschops koupensis* there is a groove medial to and leading into the fossa. In occipital view the paroccipital is seen to obscure the stapes to a smaller or greater extent.

The quadrate (Q.) shows a small to fair-sized surface when viewed at right angles to the plane in which the alveolar borders of the maxillaries lie. Its ventral edge has two fairly strong oval knobs, separated by a notch, which form the articulatory condyles for the reception of the articular. In its dorsal part the posterior face of the quadrate is overlapped by the distal end of the paroccipital firmly applied to it. Medially the short anterior process of the quadrate is overlapped by the distal end of the quadrate ramus of the pterygoid, which is firmly applied to it and which passes further backwards on to the posterior face of the quadrate above the internal cotylus. Above the pterygoid the postero-distal process of the stapes abuts securely against the posterior face of the quadrate. Just below or just distal of the postero-distal corner of the stapes there is a distinct low mound on the quadrate.

Dorso-laterally the quadrate meets the quadratojugal and along the suture these two bones are notched to form a fair-sized rounded quadratic foramen.

The quadratojugal (Q.J.) in this view presents a low but broad face between the suture with the quadrate and the edge of the downsweeping overlapping squamosal.

The stapes (St.) is, in occipital view, obscured by the paroccipital, slightly in *Moschops capensis* but greatly in *Avenantia* and *Moschops koupensis*. It is a moderately strong rod-like element with a slight waist and an expanded distal end, and is in its middle portion pierced by a large oval stapedial foramen. Its postero-distal process, directed towards the tubercle on the quadrate, is applied to the inner part of the posterior face of the quadrate, and this is firmly wedged in between the paroccipital above and the quadrate ramus of the pterygoid below. Proximally the footplate of the stapes passes anteriorly to the downwardly directed medio-ventral corner of the paroccipital to fit into the ventrally situated *fenestra ovalis*.

The stapes lies diagonally with its proximal end appreciably higher than its distal end.

The Ventral Surface of the Skull

The occiput being sloping, with its dorsal edge lying well posterior to its ventral border, is visible in ventral view. Post-mortem dorso-ventral pressure in the rock tends to accentuate this slope and in figures 9 and 11 correction to neutralize this should be allowed for.

Except for a slight upward tilt anterior to the transverse pterygoidal rami, the palate and *basis cranii* lie in practically the same plane, with the weak to fairly weak lateral pterygoidal rami lying moderately far below this plane and the suspensorium lying still further ventrally.

The articulating condyles of the quadrates lie far to very far anteriorly in a plane far anterior to the basioccipital condyle, nearly half-way up the ventral surface of the skull. The subtemporal fossae are small, short, but fairly wide; the *choanae* are fairly short but wide; the interpterygoid vacuity is a fairly narrow and short slit anteriorly bounded by the prevomer and there is a very small suborbital foramen on the suture between the palatine and transversum.

The basioccipital (B.O.) is, in ventral view, seen to form the greater part of the occipital condyle. The whole condyle is usually a more or less rounded strong knob, but in some cases it is more pear-shaped and even triangular in outline.

The basioccipital forms the anterior and medial portion of the condyle but in *Avenantia* the exoccipitals meet each other posteriorly. The notochordal pit faces postero-ventrally and the skull would in life hang downwards from its articulation with the atlas.

Anterior to its condylar part the basioccipital has a short but fairly wide to wide face which lies on a higher level than the condyle. This face is only slightly tilted downwards anteriorly and thus meets the basisphenoid in a very large angle. In its median part the basioccipital carries a pair of anteriorly converging tuberous ridges in *Moschops koupensis*, which tend to coalesce in *M. capensis* to form a low keel whereas in *Avenantia* two weak ridges are developed anteriorly with the posterior part of the surface flat.

Anteriorly the basisphenoidal tubera underlie the basioccipital which is met in a slightly concave transverse suture.

Laterally the basioccipital forms the thickened ventral rim of the *fenestra ovalis*, which thus lies far ventrally. Further backwards it abuts against the paroccipital and is underlain by the antero-medial process of the paroccipital, which forms the posterior part of the rim of the *fenestra ovalis*, and still farther backwards it is underlain by the thin sheet of the exoccipital.

The basisphenoid (B.S.) carries a low but fairly sharp median keel, lateral to which there are two posteriorly diverging fairly strongly swollen tubera (flattish in *Avenantia*); postero-lateral to the tubera the basisphenoid forms the anterior border of the *fenestra ovalis*.

Anteriorly the basisphenoid tapers and is wedged in between the quadrate rami of the pterygoids and its median keel is continued anteriorly by those of the two pterygoids. Immediately anterior to the tubera and lateral of the median keel lie the internal carotid foramina and lateral to the tubera lie the external carotid foramina.

In general the ventral faces of the basisphenoid and basioccipital lie in nearly the same plane, as these faces subtend only a very obtuse angle because the anterior part of the basioccipital is only very weakly inclined downwards in anterior direction.

The paroccipital (P.Oc.) is a large, strong and massive bone which forms a firm and strong connecting link between the cranial base and the laterally situated quadrate, squamosal and tabular. Medially the paroccipital abuts firmly against the basioccipital and is underlain by the thin flange of the exoccipital; its antero-median corner usually forms a strong process, strongly thickened where it forms the ventral and posterior parts of the rim of the *fenestra ovalis*. Its antero-lateral corner is very firmly applied to the postero-median face of the quadrate, and here the postero-distal process of the stapes is firmly wedged in between it and the quadrate. Its postero-lateral corner overlaps and is firmly applied to the medio-posterior face of the squamosal just medial of the 'auditory ridge', and also meets the ventral process of the tabular. (But in *Avenantia* the lateral end of the supraoccipital is intercalated between the paroccipital and the tabular.) Posteriorly it meets the supraoccipital on both sides of the small slit-like posttemporal fenestra in *Avenantia* and *Moschops capensis*, but only medially of this fenestra in *Moschops koupensis*.

Concomitant with the forward shift of the quadrate condyles the paroccipital has rotated on its long axis with the result that it presents a much greater face in ventral view than it does in occipital view.

The antero-ventral edge of the paroccipital is free and rounded and forms the posterior border of the fairly large fenestra lying between the basisphenoid, quadrate ramus of the pterygoid, quadrate and paroccipital.

On the suture between the paroccipital and the exoccipital lie two small foramina, the anterior being the jugular foramen and the posterior one for the exit of the tenth nerve.

The pterygoid (Pt.) is a bone of moderate size and with its fellow forms the middle portion of the ventral surface of the skull. Its most prominent components are a strong, deep but short quadrate ramus and a short and fairly weak transverse ramus. In the median line its antero-posterior length is short mainly because there is little left of the anterior process, which is so well developed in the ancestral Pelycosaurs and contemporary Therapsids.

Anteriorly the pterygoids are separated in the median line by a long and fairly open interpterygoid slit; posterior to this the pair of pterygoids meet to form a sharp keel which is posteriorly continued on the basisphenoid; the pterygoid keel is wedged into the basisphenoid.

Lateral to this median keel the pterygoid is deeply excavated and becomes very thin to form a wide and deep groove lying diagonally in the skull; in this groove the pterygoid meets the basisphenoid along a diagonally directed, fairly straight suture. This deep groove is laterally bounded by the prominent quadrate ramus, which is a deep sheet of bone lying nearly at right angles to the plane of the palate; above, where it meets the basisphenoid, it is thin, but its ventral edge is thickened and rounded and thus forms a strong girder, which posteriorly supports the quadrate.

The quadrate rami are short and diverging in posterior direction; each is firmly applied to the mesial face of the short anterior process of the quadrate and its extremity extends well posterior to the quadratic condyles. The upper edge of the end of the ramus lies below and overlaps the anterior part of the distal end of the stapes, which passing above it is firmly abutted against the mesial face of the quadrate. The quadrate ramus is connected with the lateral ramus by a strong, thickly rounded web of bone and it is here that part of the pterygoid muscle was attached. The edge of the quadrate ramus and of this web of bone form the mesial and anterior border of the subtemporal fenestra.

The lateral ramus of the pterygoid is weak, does not descend much ventrally nor extend much laterally. In *Avenantia* its ventral edge is narrow and sharp, in *Moschops capensis* it is a little thicker and in *Moschops koupensis* laterally swollen; postero-medially its edge curves to join the median keel. Laterally the ramus is met by the transversum and anteriorly by the palatine, and it has a small contact with the prevomer in the median line.

The transversum or ectopterygoid (Tr.) is a fairly small but quite strong bone linking the transverse ramus of the pterygoid with the bones of the side-wall of the skull; it is firmly joined to the inner face of the jugal and flanked by the maxilla; anteriorly its edge meets the palatine and here there is a small suborbital foramen. Due to the forward position of the transverse ramus the transversum lies lateral and even somewhat posterior to the extremity of the ramus, whereas primitively it lies anterior to the ramus.

The palatine (Pal.) is short and extends antero-laterally from its contact with the pterygoid as a sheet of fairly thick bone to form much of the lateral border of the *choana* and a varying part of its posterior border; it is laterally applied to the inner maxillary face, where it flanks the alveolar border. In the

median line a tongue of the prevomer prevents it from meeting its fellow; here the palatine carries a low mound of varying shape which is not dentigerous. In *Avenantia* this mound is continued on to the short anterior ramus of the pterygoid.

The prevomers (vomers P.V.) are strong but short bones which together form a massive interchoanal bar. Their anterior bevelled edges are applied to the inner face of the premaxillaries. Posterior to the *choanae* they widen to meet the palatines and in the median line they lie between the mesial edges of the palatines and meet the pterygoids. Anteriorly along the median line there is a groove and along the lateral edge there is an undulating ridge. Dorsally the prevomers form a narrow median ridge which is posteriorly continued by the pterygoids as part of a median septum.

The premaxillary (P.M.) has a massive alveolar face and although poorly exposed in most specimens, appears always to have housed three fairly large teeth, with indications, in some specimens, of replacing teeth lying lingually.

The maxilla (M.) has the anterior part of its alveolar border massive and wide but in posterior direction it tapers fairly rapidly and, posterior to the teeth, the maxillary edge is continuous with the sharp ventral edge of the jugal. Little is known of the teeth, but the anterior ones are large and they then rapidly decrease in size backwards. There would appear to be from ten to possibly thirteen maxillary teeth.

The jugal (J.) shows, besides its internal face which is anteriorly overlain by the transversum, a sharp to somewhat rounded ventral edge, which curves downwards to have its end abutted against the quadratojugal in *Moschops* with a nick at the junction in some skulls; but in *Delphinognathus* there is a wide and deep notch preventing the ventral edges of the jugal and quadratojugal from meeting, but these bones do meet at a higher level. The squamosal is never wholly intercalated between jugal and quadratojugal as in some of the advanced Pelycosaurs and most other Therapsids.

The quadrate (Q.) in ventral view presents its articulatory surface as a very prominent feature. The quadratic condyle is bipartite, with two fairly robust ovoid cotyli separated medially by a shallow open groove. The edges of both cotyli in ventral view overhang both the anterior and posterior faces of the upper part of the quadrate. The short anterior quadratic process lies obliquely in the skull, being directed antero-internally; it is against the mesial face of this process that the quadratic process of the pterygoid is very firmly applied. Lateral to the outer cotylus there is a step up before the quadrate meets the quadratojugal in a fairly long and nearly straight suture. A third of the way up along this suture lies a fairly small *foramen quadrati*. Due to the forward inclination of the quadrate much of its posterior face can be seen in ventral view. On this otherwise featureless face there is a small low tubercle lying some distance above the inner cotylus. More medially the quadrate receives the distal surface of the stapes firmly applied to it. In ventral view it is evident how firmly the more dorsal part of the posterior face of the quadrate is

overlapped by the downsweeping process of the squamosal and more internally by the robust quadratic process of the paroccipital, which is here also wedged in between the two faces of the postero-lateral stapedial process

The quadratojugal (Q.J.) is seen, in ventral view, to be a fairly small bone wedged in between the outer face of the quadrate and the lower overlapping edge of the downsweeping process of the squamosal A small *foramen quadrati* notches the mesial edge of the quadratojugal a third of the way up along the quadrate-quadratojugal suture.

The squamosal (Sq.) is seen, in ventral view, to form the postero-lateral corner of the skull, and sweeping downwards and forwards overlaps on to the posterior faces of the quadrate and quadratojugal. Internally the squamosal meets the paroccipital ventrally and the tabular dorsally. Near its junction with the paroccipital and the tabular the squamosal carries a fairly to very prominent 'auditory ridge' with an 'auditory groove' lying lateral to this ridge.

The stapes (St.) lies more or less obliquely in the skull. From its proximal end, which fits into the ventrally situated *fenestra ovalis*, it is inclined both forwardly and downwardly to abut against the quadrate. In ventral view the stapes shows two faces, viz. a ventral and a posterior. The ventral surface is elongate with a central waist and expanded ends. The proximal end is knob-like and is firmly fixed into the *fenestra ovalis* which is situated low down in the skull; the distal expansion has a long tapering postero-lateral process, the extremity of which is applied to the low tubercle on the posterior face of the quadrate; more anteriorly the main surface of the distal end abuts firmly against the quadrate and is here wedged in between the quadrate and the quadratic process of the pterygoid and the quadratic process of the paroccipital. The posterior face of the stapes, which is pierced by a fairly large oval stapedial foramen, is triangular in outline with its base applied to the quadrate after passing above the quadratic process of the paroccipital, which wedges the stapes firmly against the quadrate. The distal end of the stapes is thus seen to be firmly wedged against the quadrate with but little possibility of movement.

The tabulars (T.), interparietal (I.P.) and the supraoccipital (S.O.) are to a greater or less extent visible in ventral view because of the variable forward inclination of the occipital surface from above downwards.

These bones lie more or less posterior of the basioccipital condyle with the interparietal and the two tabulars forming the posterior edge of the skull. In ventral view the posterior edge is slightly concave in *Avenantia* but gently concave in *Moschops*.

Taxonomic

Moschopidae

Skull characters of the family

Skull of medium size (length 308–423 mm.; breadth 200–395 mm.) relatively short and broad to long and narrow (length varies from 105 to 182 per cent of the breadth); relatively low to fairly high (height varies from

55 to 80 per cent of the width); snout very short to fairly short (snout length varies from 45 to 61 per cent of the total skull length); the snout is fairly high to high and fairly narrow to broad (height of snout from 81 to 156 per cent of the width of the snout).

The orbit does not lie wholly in the posterior half of the skull except in *Delphinognathus*.

The transition from the facial to the cranial surface is by a gentle, even curve and never by an abrupt step. There is no depression in the surface of the nasal as in the Tapinocephalidae. The dorsal cranial bones are moderately to strongly pachyostosed (except in *Delphinognathus*) with the centres of thickening coalesced and running into the thickening of the dorsal facial bones.

The postorbital bar is fairly slender and light to very wide and massive; the postfrontal does not form a prominent boss but its surface curves evenly on to the dorsal surface. The temporal fossa is fairly small to small with its antero-posterior diameter fairly small to very small. The inter-temporal region is narrow to wide (54–172 mm.) with the parietals entering the upper border of the temporal fossa. The frontal is not excluded from the orbital border; the lacrimal has no contact with the nasal. The quadrate ramus of the pterygoid is very short. The dentition is well developed but undifferentiated.

Moschops

Skull characters of the genus

The preorbital length is 45–49 per cent of the total median length and the orbit does not, thus, lie wholly in the posterior half of the skull; the snout is thus short (preorbital length 160–190 mm.) and fairly broad to broad (156–227 mm.) and fairly low to fairly high (108–162 mm.) with the height 74–95? per cent of the width.

The dorsal cranial bones are strongly pachyostosed.

The prefrontal is greatly thickened and this is confluent with the pachyostosis of the nasal and frontal, but this does not greatly overhang the orbit although the orbital border is thick.

The area around the pineal foramen is greatly thickened but does not stand out above the general skull surface.

The postorbital bar is fairly to very wide and moderately to very massive.

The posttemporal arch is moderately to very thick and massive and the temporal fossa is moderate to small with its antero-posterior diameter fairly to very greatly reduced.

The dorsal parietal surface is broad to very broad (142–172 mm.) and the interorbital width is 70–100 per cent of the intertemporal width.

The intersquamosal width is moderate to great (210–395 mm.) and the median length is 103–159 per cent of the width. (The low figure for the width in one specimen is undoubtedly due to lateral compression and the average

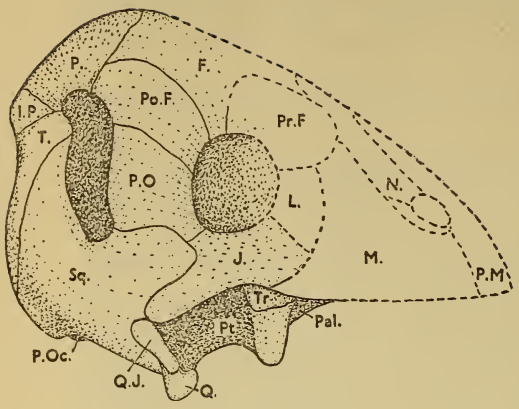


FIG. 1

Moschops capensis. Lateral view of the posterior two-thirds of a skull from Kruisvlei, Beaufort West. S.A.M. 11972. × 1/6. Note. All the figures in this paper are projections and not perspective drawings. *Lateral view* indicates an orthoprojection of the lateral surface on to the median (sagittal) plane; *dorsal view*—the dorsal surface projected on to the plane in which the alveolar borders of the maxillaries lie; *occipital view*—the occiput projected on to a plane at right angles to the above two; *ventral view*—a projection on to the plane in which the alveolar borders of the maxillaries lie.

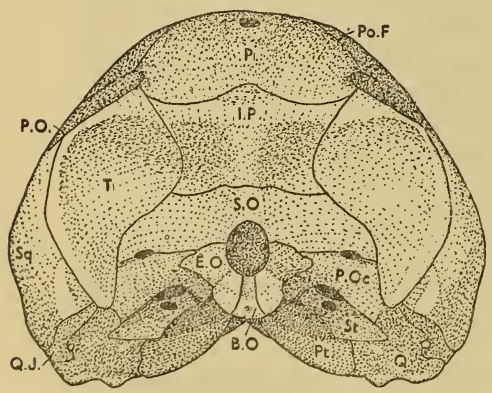


FIG. 2

Moschops capensis. Occipital view of S.A.M. 11972 × 1/6.

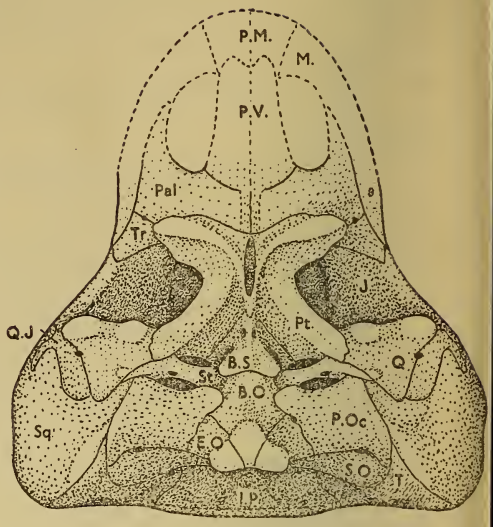


FIG. 3

Moschops capensis. Ventral view of S.A.M. 11972 × 1/6.

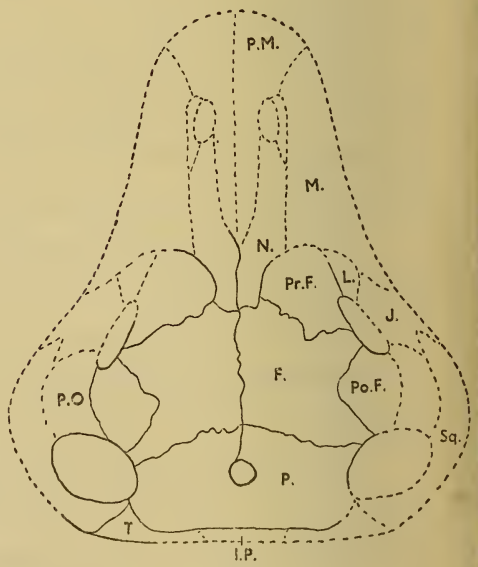


FIG. 4

Moschops capensis. Dorsal view of an imperfect skull from Groot Kruidfontein, Prince Albert. S.A.M. 5010. × 1/6.

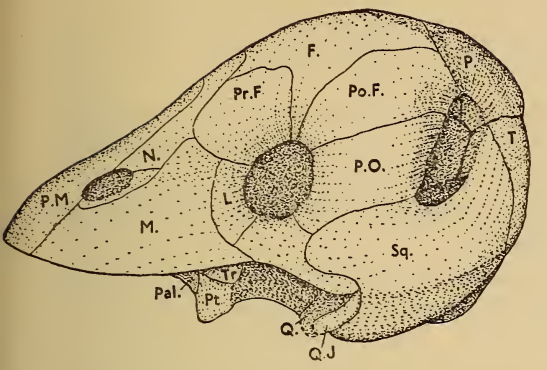


FIG. 5

Moschops koupensis nov. sp. Lateral view of a very good skull from Die Krans, Prince Albert. S.A.M. 11582. × 1/6.

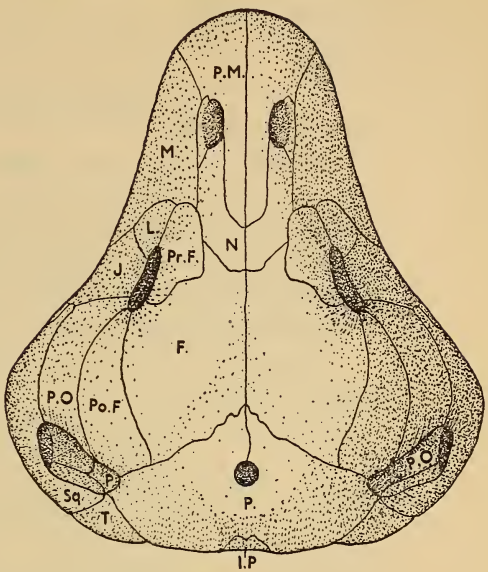


FIG. 7

Moschops koupensis nov. sp. Dorsal view of S.A.M. 11582 × 1/6 with the bilateral symmetry restored.

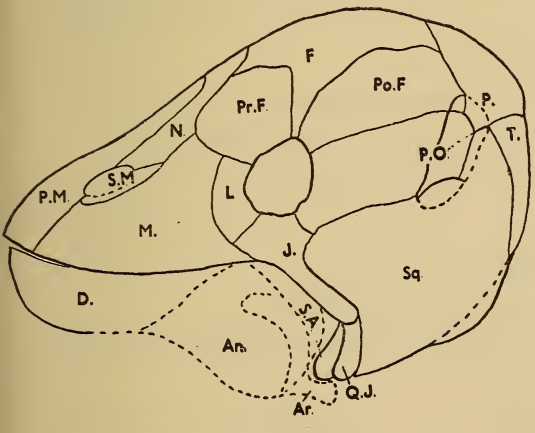


FIG. 6

Moschops koupensis nov. sp. Lateral view of S.A.M. 11582 × 1/6 with the slight dorso-ventral compression corrected.

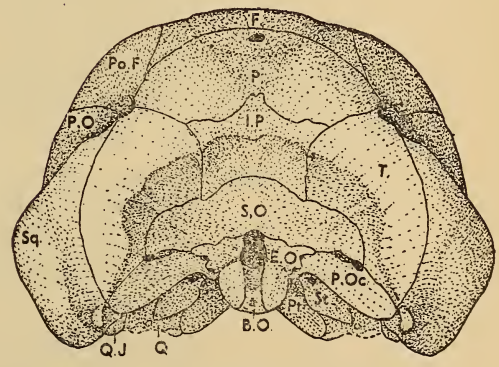


FIG. 8

Moschops koupensis nov. sp. Occipital view of S.A.M. 11582 × 1/6 with the symmetry restored, but not the effects of a slight dorso-ventral compression.

proportion appears to be about 112 per cent.) The *Moschops* skull is thus fairly short and broad.

Genotype

Moschops capensis, Broom 1911 (figs. 1–4)

Specific diagnosis:

Medium to wide across parietals, with the interorbital width 73–100 per cent of the intertemporal width. Snout relatively wide. Occipital surface unreduced and transverse pterygoidal rami weak.

Holotype A.M.N.H. 5550. Nearly complete skull with mandible which probably belongs to the same individual.

Spitskop Laingsburg Low ? *Tapinocephalus* zone Coll. Whaits.

Topotypes A.M.N.H. 5551–5557. Parts of eight skeletons.

Referred specimens:

S.A.M. 5010. Posterior two-thirds of a skull. Groot Kruidfontein, Prince Albert.
Low *Tapinocephalus* zone. Coll. Haughton.

S.A.M. 11291. A practically complete skull but distorted by dorso-ventral compression.
Kruisvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11295. A fairly good posterior two-thirds of a skull.
Koringplaas, Laingsburg.
Low ? *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11970. Substantial pieces of ten separate skulls showing various parts of the cranial structure.
Kruisvlei, Beaufort West.
Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11972. An excellent occiput and posterior half of a skull.
Kruisvlei, Beaufort West.
Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11973. Good posterior two-thirds of a skull.
Kruisvlei, Beaufort West.
Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11974. A good skull which has been subjected to a little dorso-ventral pressure.
Kruisvlei, Beaufort West.
Low *Tapinocephalus* zone. Coll. Boonstra.

Moschops koupensis sp. nov. (figs. 5–9)

Specific diagnosis:

Very wide across the parietals with the interorbital width 70 per cent of the intertemporal width. Snout relatively narrow. Occipital surface greatly

reduced by overgrowth from above and from the sides. The transverse pterygoidal rami are strong.

Holotype S.A.M. 11582. A very good skull with part of the mandibles. Die Krans, Prince Albert.

Low ? *Tapinocephalus* zone. Coll. Boonstra and Botma.

Delphinognathus

Skull characters of the genus

The preorbital length is 61 per cent of the total median length (as reconstructed); the snout is thus apparently fairly long (preorbital length 195 ? mm.) and it is narrow (125 ? mm.) and fairly high (108 mm.) with the height 86 per cent of the width. The dorsal cranial bones are not very strongly pachyostosed.

The prefrontal is not greatly thickened.

The area around the pineal foramen is greatly raised to form a conical mound standing well above the general dorsal surface.

The postorbital bar is fairly narrow and lightly built.

The posttemporal arch is apparently fairly narrow and lightly built and the temporal fossa is fairly large with its antero-posterior diameter not greatly reduced.

The dorsal parietal surface is only moderately broad (120 mm.) and the interorbital width is 96 per cent of the intertemporal width.

The intersquamosal width is apparently fairly small (200 mm. as reconstructed) and the median length is probably about 160 per cent of the width and the skull is thus relatively long and narrow.

There is a very distinctive notch between the jugal and the quadratojugal.

Genotype

Delphinognathus conocephalus, Seeley 1892 (fig. 10)

Specific diagnosis as for the genus.

Holotype S.A.M. 713. An incomplete, somewhat distorted skull.

Locality unknown, but probably from high up in the *Tapinocephalus* zone near Beaufort West. Coll. T. Bain.

Referred specimens:

S.A.M. 11971. A fair skull much distorted by lateral pressure. Kruisvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Avenantia

Skull characters of the genus

The preorbital length (as reconstructed) is 45 per cent of the total median length and the orbit thus does not lie wholly in the posterior half of the skull; the snout (as reconstructed) is thus short (preorbital length 174 mm.) and broad (210 mm.) and fairly low (126 mm.) with the height 60 per cent of the width.

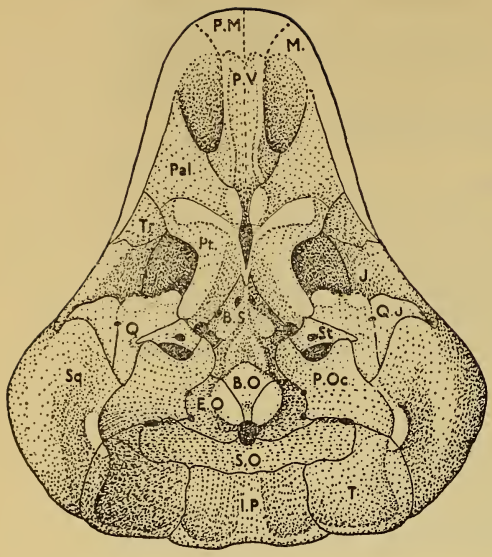


FIG. 9

Moschops koupensis nov. sp. Ventral view of S.A.M. 11582 × 1/6, with symmetry restored, but the slight forward shift of the suspensorium due to some dorso-ventral pressure is not corrected.

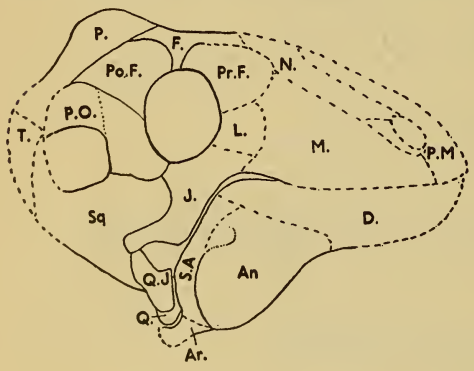
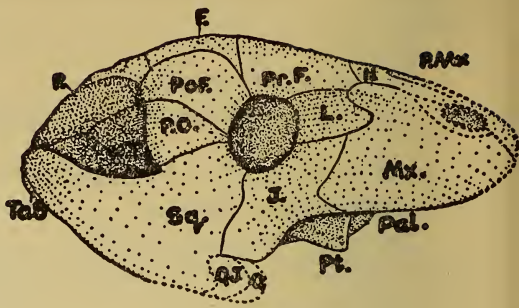


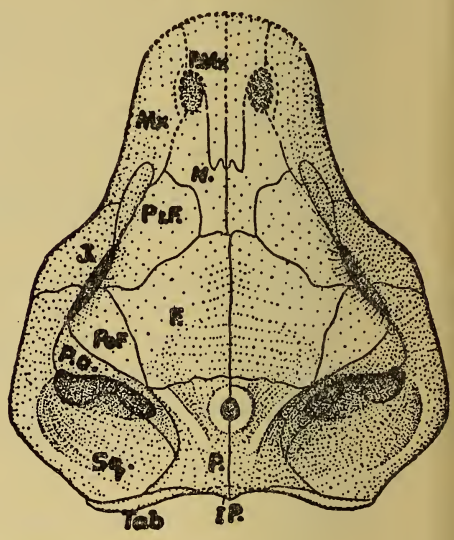
FIG. 10

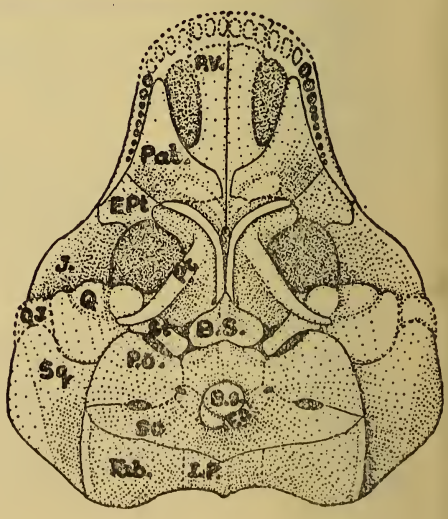
Delphinognathus conocephalus. Lateral view of the type skull S.A.M. 713 × 1/6, clearly showing the notch between the jugal and the quadratojugal.

FIG. 11 →

Avenantia kruisvleiensis. The type skull S.A.M. 9166 × 1/6: Top-lateral view; middle-dorsal view; bottom-ventral view. The symmetry has been restored but more allowance should have been made for the effects of the dorso-ventral pressure that the skull has undergone. This applies mainly to the too forward position of the suspensorium.







The dorsal cranial bones are strongly pachyostosed (but moderate in the intertemporal region and along the median line).

The prefrontal is greatly thickened and this is confluent with the pachyostosis of the nasal and frontal, but this does not greatly overhang the orbit although the orbital border is fairly thick.

A well-defined ringwall is developed round the pineal foramen, but this does not rise well above the general dorsal surface.

The postorbital bar is moderately wide and massive.

The posttemporal arch has its upper edge narrow and lightly built and the temporal fossa is fairly large with a large antero-posterior diameter.

The dorsal parietal surface is narrow (54 mm.) with the development of a low crista curving down posteriorly, and the interorbital width is 333 per cent of the intertemporal width.

The intersquamosal width is great (348 mm.) and the median length (as reconstructed) 112 per cent of the width and the skull is thus short and broad.

Genotype

Avenantia kruisvleiensis, Boonstra 1952 (fig. 11)

Specific characters as for the genus.

Holotype S.A.M. 9166. A good skull lacking only the tip of the snout and the lower jaw.

Kruisvlei, Beaufort West.

Low *Tapinocephalus* zone. Coll. Boonstra.

Moschognathus

Skull characters of the genus

Only fragments of the skull and a good mandible are known, but much of the postcranial skeleton is preserved. No skull characterization can thus be given here.

Moschognathus whaitsi, Broom 1914

Holotype A.M.N.H. 5602. Good mandibles with which are associated part of the skull and much of the skeleton.

Beaufort West district.

High ? *Tapinocephalus* zone. Coll. Whaits.

Pnigalion

Skull characters of the genus

The dorsal cranial bones are not very strongly pachyostosed. The area around the pineal foramen is thickened to form a low mound standing above the general dorsal surface. The postorbital bar is not wide and is fairly lightly built. The posttemporal arch is moderately wide and massive and the temporal fossa is fairly large with its antero-posterior diameter not much reduced. The dorsal parietal surface is only moderately broad (120 mm.). The intersquamosal

width is fairly great (375 mm.). The quadratojugal as identified by Watson (1914) shows a large squarish outer face. There is a distinctive step at the junction of the squamosal and tabular.

Genotype

Pnigalion oweni, Watson 1914

Holotype B.M.(N.H.) R3596. A good posterior two-thirds of the skull and dentaries.

De Cypher, Beaufort West.

Low *Tapinocephalus* zone. Coll. Seeley.

Moschoides

Skull characters of the genus

As only part of the lower jaw is known no skull characterization can be given.

Genotype

Moschoides romeri, Byrne, 1937

Holotype. Walker Museum, Chicago. A fairly good skeleton.

Hottentotsrivier, Beaufort West.

Low ? *Tapinocephalus* zone. Coll. Romer and Miller.

Discussion

As the cranial material of *Moschognathus*, *Pnigalion* and *Moschoides* is so inadequate and as, moreover, they could very well at this stage be considered co-generic with *Moschops*, only three Moschopid genera, viz. *Delphinognathus*, *Moschops* and *Avenantia*, need be discussed here.

In the genus *Moschops* the more heavily built or more pachyostotic skulls may be considered to represent either (*a*) males or (*b*) mature and old individuals male or female, and the more lightly built or less pachyostotic skulls to be of either (*a*) females or (*b*) juveniles of either sex.

Now, in the Deinocephalia generally it is clear that in the more primitive forms (*Moschosaurus*, *Agnosaurus*, *Delphinognathus*) there is little pachyostosis and in the more advanced forms the pachyostosis becomes more and more developed. The pachyostosis is thus a phyletic feature. But within certain species there is also sufficient evidence that the pachyostosis is also a function of age in the individual. There is, however, little real evidence that the pachyostosis is sexually determined.

Thus, the degree of pachyostosis in those skulls referred to the genus *Moschops* should be considered to be dependent on age only.

In the known two skulls of *Delphinognathus* the pachyostosis is moderate, being chiefly confined to the conical mound around the pineal foramen and a little thickening of the supra- and postorbital borders. There is practically no

thickening, or very little, in the posttemporal, postorbital and infratemporal and infraorbital arcades.

Now, in no lightly built *Moschops* skull do we find this localization of the pachyostosis, these skulls being only slightly larger than that of *Delphinognathus*. If the lightly built *Moschops* skulls are correctly considered to be those of young animals then *Delphinognathus* cannot be considered a juvenile of *Moschops* and is thus rightly considered to be a distinct genus.

In *Avenantia* the pachyostosis is well developed in the postorbital bar, the dorsal and dorso-anterior orbital rim and the roof bones up to the frontoparietal suture. But in the parietal region the pachyostosis is little developed, the posttemporal arch remains lightly built and the temporal fossa remains roomy. No process of simple ageing can possibly be thought capable of transforming the *Avenantia* skull into a *Moschops* skull.

Efremov (1940) has maintained that the *Moschops* skull is a growth stage of *Mormosaurus* with *Tapinocephalus* as the final product. He does not mention the Struthiocephalids and one wonders where he would fit them in this process of ageing.

In all the known heavy *Moschops* skulls the sutures are closed which allows one to conclude that they are mature. But in some *Tapinocephalus* skulls the sutures are still open and these skulls are of the same size as one in which the sutures are closed. The large skulls with open sutures may thus be considered immature. They and *Moschops* cannot thus both be considered immature *Tapinocephalus*.

Moreover, in *Tapinocephalus* the dorsal and lateral borders of the occiput slightly overgrow and encroach on to the *planum occipitale* reducing its size. Now, in most heavy *Moschops* skulls there is no or very little overgrowth and encroachment, but in the skull of *M. koupensis*, which is somewhat smaller than the heavy *M. capensis* skulls, this overgrowth and encroachment is very much greater than in the very much larger skull of *Tapinocephalus*. Obviously the skull of *M. koupensis* cannot possibly be a young *Tapinocephalus*. In any case, *Mormosaurus*, with its longer snout, cannot be intermediate between *Moschops* and *Tapinocephalus* in both of which the snout is short. Similarly the long-snouted *Keratocephalus* and Struthiocephalids (except *Struthionops*) cannot be intermediate between *Moschops* and *Tapinocephalus*.

In our present stage of knowledge the Moschopids, Struthiocephalids and Tapinocephalids must be considered as distinct directions in the evolution of the Tapinocephalia.

References

Boonstra, L. D. 1936. 'Some features of the cranial morphology of the tapinocephalid deinocephalians. *Bull. Amer. Mus. nat. Hist.*, **72**, 2, 75–98.

Boonstra, L. D. 1952. 'n Uiters interessante nuwe deinocephaliër, *Avenantia kruisvleiensis*, gen. et sp. nov.' *Tydskr. Wet. Kuns*, **12**, 2, 250–5.

Broom, R. 1910. A comparison of the Permian reptiles of North America with those of South Africa. *Bull. Amer. Mus. nat. Hist.*, **28**, 20, 197–234.

Broom, R. 1911. On some new South African Permian reptiles. *Proc. Zool. Soc. Lond.*, **1911**, 1073–82.

Broom, R. 1914. A further comparison of the South African dinocephalians with the American pelycosaurs. *Bull. Amer. Mus. nat. Hist.*, **33**, 9, 135–41.

Broom, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals.* London: Witherby.

Byrne, F. 1937. A preliminary report on a new mammal-like reptile from the Permian of South Africa. *Trans. Kans. Acad. Sci.*, **40**, 221–4.

Byrne, F. 1940. Notes on the evolution of the mammal-like reptiles. *Trans. Kans. Acad. Sci.*, **43**, 291–6.

Efremov, J. A. 1940. *Ulemosaurus svijagensis* Riab.—ein Dinocephale aus den Ablagerungen des Perm der UdSSR. *Nova Acta Leop. Carol.*, N.F. **9**, 59, 155–205.

Gregory, W. K. 1926. The skeleton of *Moschops capensis* Broom, a dinocephalian reptile from the Permian of South Africa. *Bull. Amer. Mus. nat. Hist.*, **56**, 3, 179–251.

Seeley, H. G. 1892. On *Delphinognathus conocephalus* (Seeley) from the Middle Karroo beds, Cape Colony, preserved in the South African Museum, Cape Town. *Quart. J. geol. Soc. Lond.*, **48**, 469–75.

Watson, D. M. S. 1914. The Deinocephalia, an order of mammal-like reptiles. *Proc. Zool. Soc. Lond.*, **1914**, 749–86.